From meso- to macroscale population dynamics: a new density-structured approach

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Summary

1. To predict how plant populations may respond to changes in the environment or management, it is necessary to quantify the factors influencing their population dynamics and distributions over large spatial and/or temporal scales.

2. Most studies of plant population dynamics monitor demography at the sub-metre scale. Extrapolation or prediction from these studies is difficult because the data are sparse, parameter error cannot be ascertained and the data may not cover the range of expected environmental conditions.

3. Here, we describe a survey method based on density-structured models. These models use a discrete density state variable and model rates of transition between density states. Although analytically simple, these models are empirically useful as they may be parameterized using readily collected data. They also offer an empirical link between meso-scale and macro-scale population dynamics.

4. For a large-scale study on annual weeds, we describe the rapid estimation of densities using relatively coarse density estimates using visual estimates of density. Using information from detailed surveys, we describe how we use the method to measure populations of annual plants to a scale of 20 × 20 m in areas of up to 4 ha per population within 500 different arable fields over 3 years.

5. We show that the approach taken is repeatable within and among observers, and we quantify the degree of measurement error. We give examples of the resultant data, and compare these with the data obtained from nested small-scale plots. Finally, we show how the information from this type of survey can be incorporated into population models and used to measure within-population and inter-annual flux.

Key-words: modelling, observation error, population ecology, sampling, surveys, transition rate

Introduction

Understanding the dynamics of animal and plant populations, and predicting how they change over time, has been a key motivator in ecology (Lotka 1932; Krebs 1972; Begon, Townsend, & Harper 2006). Factors such as climate, soil, management and biotic interactions determine the distributions of species, and vary over large geographical scales. Forecasts of the impact of changing environments on ecological populations are consequently of strategic importance, especially considering the unprecedented changes in environment and climate (Millenium Ecosystem Assessment 2005; Sutherland 2006; IPCC 2007). A limitation, however, is that predictions are needed that apply over spatial and temporal scales far larger than can be easily studied using conventional approaches (e.g. Sutherland & Watkinson 2001). Models are an important tool in allowing us to make predictions at the relevant scales.

In plant ecology, models are frequently used, for example, in modelling the evolution of life-histories (Childs *et al.* 2003; Ellner & Rees 2003, 2005; Rees *et al.* 2006), weed ecology (e.g. Firbank 1985; Doyle, Cousens, & Moss 1986; Firbank & Watkinson 1986; Freckleton & Watkinson 1998; Maxwell & Luschei 2004) and simulating harvesting (Boot & Gullison 1995; Olmsted & Alvarez-Buylla 1995; Freckleton & Watkinson 1998, Matos, Freckleton, & Watkinson 1999; Freckleton

et al. 2003). Ideally models should be tested and be able to predict accurately the changes in dynamics and distributions of populations that may occur as a result of changes in the environment or management, alongside the degree of uncertainty in those predictions (Cousens 1995; Ludwig 1996, 1999; Ludwig, Mangel, & Haddad 2001; Clark 2003, 2005; Freckleton *et al.* 2008; Freckleton & Stephens 2009).

A large proportion of models and field studies of plant population dynamics have relied on the study and monitoring of plant densities using detailed demographic methods. The aim is to parameterize a model for population dynamics of the form (Watkinson 1980; Rees, Grubb, & Kelly 1996; Silvertown & Charlesworth 2001):

$$N(t + 1) = \lambda(t)N(t)f[N(t)] \qquad \text{eqn 1}$$

$N(t)$ and $N(t + 1)$ are the numbers or densities of plants in years t and $t + 1$, N being the state variable of the model. $\lambda(t)$ is the density-independent population growth rate in year t, and measures the rate of population growth resulting from seed production, clonal growth and survival as well as immigration and emigration. These may vary from year to year or from place to place. The function $f[N(t)]$ measures density-dependence in the population dynamics, resulting, for example, from competition between plants for resources (Watkinson 1980) or negative effects of density on germination (Lintell Smith *et al.* 1999; Watkinson, Freckleton, & Forrester 2000). A simple model of a similar form to eqn (1) can also describe the stochastic population dynamics of an annual plant with a persistent seedbank (MacDonald & Watkinson 1981; Ellner 1984).

There are several difficult stages in parameterizing a model from field data, and in using models to make predictions. One key limitation is that it is frequently impossible to obtain sufficient data to measure all parameters, or to estimate the variance in parameters resulting from spatial or temporal variability. In addition, the density-dependent function $f[N(t)]$ has to be estimated, but this requires demographic data from a range of densities and is expected to be subject to great variability (Ramula & Buckley 2009). Often it is possible to use the literature to estimate parameters, and this approach has been used in the development of models that incorporate demographic parameters from the whole life-cycle (e.g. Rees & Paynter 1997; Freckleton & Watkinson 1998; termed 'no holds barred' estimation by Caswell 2000). In other cases, the estimates are derived from local, small-scale perturbations.

An important limitation of demographic models is that there are conditions under which predictions may be suspect, particularly for populations with potentially fast rates of growth such as invasive and arable weeds (Freckleton *et al.* 2008). In such populations, models may be numerically unstable with the consequence that very small changes to parameter values may have enormous effects on model predictions. This is exacerbated if the uncertainties in model parameters are not quantified or if the uncertainty in model predictions is unsatisfactorily large (Ludwig 1996, 1999; Ludwig, Mangel, & Haddad 2001). Another complication is that data usually contain measurement error, which has to be accounted for in the model fitting process (Shenk, White, & Burnham 1998; Dennis *et al.* 2006; Freckleton *et al.* 2006). Quantifying census error is an extremely important consideration in the design of a long-term monitoring programme.

A further limiting constraint is that demographic data are relatively costly in terms of time, effort and expense (e.g. Condit 1998; Clay *et al.* 1999; Qi *et al.* 2008). As a result, most studies in ecology are usually at spatial scales of < 1 m^2, and are of short duration (Kareiva & Anderson 1988; May 1989). For example, we enumerated plot size in all papers published in *Weed Research* vol. 48 (2008). Twenty-one studies included field research, and 84% of these used sample plots smaller than 1 m^2. As plant populations are usually patchily distributed at scales exceeding this (e.g. Kunin 1998), small-scale studies have to be extrapolated if they are to predict population dynamics at relevant spatial scales.

Alternative modelling formulations exist, however. In a study predicting the population dynamics of an invasive grass, Taylor & Hastings (2004) used a 'density-structured' approach. Their approach differed from previous population models in that the state variable in this model was a discrete density state. The model then modelled the rate at which sites moved between these density states, with the parameters of the model essentially being a matrix of transition probabilities. Shea & Possingham (2000) and Bogich & Shea (2008) have applied similar approaches to metapopulation models.

Compared with eqn (1), a density-structured model has the following structure:

$$\mathbf{N}(t + 1) = \mathbf{T}\mathbf{N}(t) \qquad \text{eqn 2}$$

In eqn (2) $\mathbf{N}$ is a vector of density states, compared with the continuous density state variable in eqn (1), and $\mathbf{T}$ is a transition matrix measuring the transitions between the density states. An entry q_{ij} of matrix $\mathbf{T}$ is the probability that a site in state i in one time period will be in state j in the next. The matrix $\mathbf{T}$ summarizes the mappings between all density states, and expresses the outcome probabilistically, hence $\mathbf{T}$ encapsulates both the nonlinearity in population growth rates ($f[N(t)]$ in eqn 1) as well as the temporal stochasticity in the model parameters.

This might, initially, appear an unsophisticated approach in that population dynamics are not modelled explicitly, but instead are summarized by coarse transition probabilities. However, this modelling framework offers several empirical and analytical advantages. In empirical terms, there are two key advantages to this approach: first, the data for parameterizing a density-structured model should be relatively easy to collect as discrete density states should be easier and quicker to assign than detailed enumeration of population densities; second, the errors in the data are straightforward to assess via replicated surveys, which should be relatively quick and easy to perform. In analytical terms, these models offer four advantages: first, the transition probabilities should be statistically straightforward to estimate; second, it is unnecessary to specify an underlying model for population dynamics as the model is defined purely by the estimated probabilities, which simplifies

analysis; third, the model is a simple linear one, which has well understood properties as it is a special case of a structured model, for which considerable theory exists (Caswell 2000). Finally, such models are able to recapture and simulate the behaviour of populations accurately when compared with fully continuous models (Freckleton *et al.* 2011).

Other studies have attempted to address the shortcomings of small-scale demographic models in different ways. Remote sensing can be used to monitor communities at large spatial scales, but, to date, can only differentiate individual species if they are very different from the community matrix (Asner & Martin 2009; Huang & Asner 2009).

This density-structured modelling approach suggests that data on population dynamics in which the measured state variable is a density state, rather than an estimate of continuous density, can be used profitably in a range of modelling applications. Motivated by this, we have developed a field monitoring approach that relies on estimating density-states with a view to measuring meso-scale population dynamics rapidly and at large spatial scales.

Here, we describe the application of this method to measuring the dynamics of populations within communities of annual plants. The aims of this study were to describe and evaluate the method, and to illustrate how the approach enables meso-scale mapping of populations. We show how the data measured using this approach are robust and repeatable among observers, demonstrate that it is straightforward to quantify census error and show that we are able to use the approach to capture large-scale variation in population density successfully. Finally, we discuss how this approach can be developed further.

Materials and methods

OVERVIEW OF APPROACH

The aim of the approach is to assess densities rapidly across large areas to characterize the spatial distribution of species at a meso-scale (i.e. greater than individual or small patches of plants), and to capture within- and among-site variability simultaneously. To provide a fully integrated approach, the field methods and data collection are geared to generating rapidly large quantities of continuous, spatially explicit density-state information for each focal species. For this system to be cheap, rapid and reliable, it must: (i) accurately relocate the sample sites from year to year; (ii) accurately and repeatably assign density states (i.e. estimate the number of individuals) at each site; and (iii) reflect the biology of the study organism/s. The ability to relocate sample sites accurately and repeatably is essential if temporal changes are to be assessed. Over small, undisturbed areas, this could be undertaken with physical markers. However, in most areas, logging of differentially corrected GPS coordinates, or even overlaying a D-GPS grid, will be required to ensure relocation if markers have to be removed by others between visits.

Rather than rely on detailed counts to enumerate population size, categorical states are assigned at each sample location. Although assigning ordered plant abundance categories in small plots has a long history of study, this method is rarely used to monitor temporal change and has mostly been used to describe communities (e.g. van der Maarel 1975, 1979). These categorical density states are based on

prior knowledge of the likely population sizes to be encountered, and the likely biological significance of these. For example, density states could be assigned based on the quartiles of the population size encountered in previous individual-based plots or from a preliminary census. Fewer than ten density states are recommended to facilitate ease of assignment in the field. Even with three density states, robust estimates of population dynamics are obtained (Freckleton *et al.* 2011). Sample locations can be of any size and arranged in any way that the investigator desires, but ideally would be continuous, negating the need for a complex interpolation and easing the logistics of the census.

DATA: ARABLE WEED SURVEY

We describe an application of this approach to monitor plant populations over large spatial and temporal scales. Although we are mainly concerned in this article with outlining and validating the census methodology, in this section, we also describe the details of the whole study so that the data that this survey method generates may be placed in its wider context.

A suite of arable weed species populations has been monitored in over 500 fields in 49 farms in three UK counties from 2007. The aim of this study is to understand the ecological effects of management at the field scale, for instance, on numbers of weeds, and to link this to factors that drive management. To do this requires that weed populations are monitored at the fine scale (within field) to capture the effects of management on abundance and dynamics, as well as at the large scale (field- and farm-scale) to encompass a range of types of farming management and hence to enable a link between the variance in farmer behaviour and variation in weed population dynamics.

To cover a range of ecological and abiotic conditions, a sample of 49 farms were selected from three primarily arable lowland counties in central and eastern England: Bedfordshire, Lincolnshire and Norfolk. Approximately ten fields that would be in rotation for the subsequent 3 years were chosen in consultation with the farmer, to reflect the range of farm soil conditions and crop rotations.

Weed populations were censused three times a year, in the spring (crop seedlings), summer (mature, pre-harvest) and autumn (crop stubbles, and any mature weeds in late-harvest crops such as sugar beet). To set up the survey, in autumn 2006 and spring 2007, each field was visited and several tractor wheelings were mapped using a D-GPS unit [MobileMapper CX, Thales (now Magellan)]. Using the GIS software package MapMaker (http://www.mapmaker.com), grids with 20 × 20 m numbered cells were drawn over each field to cover at least 2 ha, parallel with the tractor wheelings. Pilot surveys showed that 20 × 20 m provided a good trade-off between coverage and precision; ensuring that the grid is parallel to the tractor wheelings aids both walking the fields, and locating the grid cells for ease of data collection. In subsequent censuses, the density of focal weed species in each cell of the grid was recorded on paper maps by one to four fieldworkers walking in parallel up and down the tractor wheelings. Location within the field, and grid cell was determined using DGPS (online Fig. S1).

Density-states for each study species were assigned using the quartiles of densities determined in the Farm Scale Evaluation of GM crop trials, the most extensive survey of weed populations in the UK to date (Table 1, online Fig. S2, Heard *et al.* 2003). The study species were chosen to reflect ecologically important species, economically harmful species, tall, easily seen species, and small-statured species, as well as a mixture of monocot- and dicotyledons (Table 1).

It would have been ideal to conduct replicated surveys routinely to assess the impacts of observer and measurement error. However,

Table 1. The study species in the arable weed survey

Species	Family	Common name	Quartiles of density distribution*			Stature	Importance
			25%	50%	75%		
Alopecurus myosuroides Huds	Poaceae	Blackgrass	160	450	1450	High	Economic
Avena fatua L.	Poaceae	Wild-oat	60	60	170	High	Economic
Chenopodium album L.	Chenopodiaceae	Fat-hen	114	230	630	High	Ecological
Fallopia convolvulus (L.) Á. Löve	Polygonaceae	Black bindweed	60	114	286	Low	Ecological
Papaver rhoeas L.	Papaveraceae	Common poppy	60	170	470	High	Visual
Poa annua L.	Poaceae	Common meadow-grass	400	1430	4614	Low	Ecological
Stellaria media L.	Caryophyllaceae	Common chickweed	114	340	1030	Low	Ecological

*Density states are assigned as follows: $0 > L < 25\%$ L; $25\% > M < 50\%$; $50\% > H < 75\%$; $75\% > V$, values are per 20 m^2.

given that it took 5–6 weeks for two fieldworkers to make single passes through all sample fields, the resources for routine replication were insufficient. We therefore conducted a subset of replicated surveys intended to provide this information as well as validate the methods used, which are described in this article.

We conducted three stages of analysis. First, we compared our density-state approach to an individual-based approach where we counted all the individuals within 1 m^2 quadrats in the larger 20×20 m cells. Second, we compared within and between observer error in density estimates in two situations, a simple binomial (weed is present or absent) situation, followed by a more complex multi-state situation. Finally, we estimated how errors in assigning density states affected the estimates of transition probabilities for a cell in year t to year $t + 1$.

COMPARISON OF DENSITY-STATE AND INDIVIDUAL-BASED APPROACHES

To demonstrate that density states were reliable indicators of local density, fields containing a wide range of weed densities were targeted for more detailed surveys. Six 1×1 m quadrats were placed within randomly selected 20×20 m cells using x–y coordinates generated from a random number table. The number of individuals was then recorded for each small quadrat. We concentrated this survey effort on two of the key species in this system, *Alopecurus myosuroides* Huds. and *Chenopodium album* L.

In the case of *A. myosuroides,* we studied 1530 1×1 m plots in 255 20×20 m quadrats across 11 fields of winter wheat on six farms, whilst 450 1×1 m plots were studied in 75 20×20 m quadrats within six fields on four farms for *C. album.*

We analysed the data using generalized linear models in which the response variable was the total count of weeds in the six 1 m^2 samples within each 20×20 m quadrat; field and density state were main effects, together with the density state × field interaction. We were particularly interested in the interaction term because this measures whether the assigned density states are repeatable (with respect to mean quadrat density). We used quasipoisson error to deal with over-dispersion.

QUANTIFICATION OF OBSERVER ERROR

To determine the census error inherent in assigning density states, we conducted replicated surveys. As emphasized above, quantifying the degree of survey error is essential as errors can lead to bias in parameter estimates and predictions (Freckleton *et al.* 2006; Royle &

Dorazio 2008). We conducted a series of studies to estimate the variance in data resulting from measurement error using a subset of the weed study species. We first conducted a study to measure the variance in density assignments between observers and subsequently examined how this variance differed among surveys conducted at different times and in different fields.

Binomial dataset

In the first replicated surveys, two observers independently surveyed a field of winter wheat in the summer of 2007, and fields of winter wheat and spring barley in the summer of 2009. The only weeds present in each field were *A. myosuroides* and *Avena fatua* in one of two density states (absent or low density). As detailed below, this allows a simple analysis of the effects of inter-observer variability that can be built upon to analyse more complex data.

Multi-state dataset

In the second set of analyses, we used data from autumn 2008 and summer 2009 from fields where the range of densities was much greater. In the autumn of 2008, three sugar beet fields were censused in which the predominant weed was *C. album*. Two observers censused each field independently, and the survey was repeated on two separate days (18 and 19 October 2008). This weed was at a high density and widely distributed in these fields. Prior to harvest in the summer of 2009, fields of winter wheat ($n = 2$), oil seed rape (1), spring barley (2) and field bean (1) were censused by two observers independently (23 and 24 July 2009). The bean and wheat fields were re-censused the following days.

STATISTICAL ANALYSIS

Analysis of replicated surveys – binomial dataset

In the first dataset, only density states 0 (absent) and 1 (low density) were recorded. The states recorded by the observers are estimates of the true state, which is unknown. From these data, we aimed to estimate the frequency with which density states are misclassified, as well as the frequencies of the density states. Note that the latter cannot be estimated directly from the data as in the presence of measurement error, estimated frequencies could be biased (see below).

The probability of correctly classifying states 0 and 1 are denoted P_{00} and P_{11}, respectively. The probability of misclassifying state 0 as state 1 is P_{01} and the probability of misclassifying state 1 as state 0 is

P_{10}. The frequencies of 0 and 1 are f_0 and f_1, respectively. The data consist of pairs of density state estimates and we model the probability of observing a given outcome, given this set of parameters. Thus, the probabilities of observing a pair of estimates that are both 0, both 1, or 0/1 are:

$$P(0,0) = P_{00}^2 f_0 + P_{10}^2 f_1 \qquad \text{eqn 3a}$$

$$P(1,1) = P_{11}^2 f_1 + P_{01}^2 f_0 \qquad \text{eqn 3b}$$

$$P(0,1) = 2P_{00}P_{01}f_0 + 2P_{10}P_{11}f_1 \qquad \text{eqn 3c}$$

For n pairs of observations (s_1, s_2), these probabilities can be used to compute the log-likelihood of the data given the parameters:

$$L = \sum_{i=1}^{n} \ln P(s_i, s_j) \qquad \text{eqn 4}$$

To generate maximum likelihood estimates of the parameters, we note that $P_{01} = 1 - P_{00}$, $P_{10} = 1 - P_{11}$ and $f_0 = 1 - f_1$. There are therefore three parameters to be estimated (P_{01}, P_{10} and f_0). The three parameters cannot be estimated simultaneously, however, as the parameters are not uniquely identifiable. This is a well-known problem in the analysis of such data (e.g. Bross 1954; Royle & Link 2006) and can be resolved only by providing additional information, typically the true value of f_0. For our data, f_0 is not easily estimated, however, as estimating the exact density state without error for each quadrat within a field requires enormous time. Therefore, we made two reasonable assumptions to fit this model.

To estimate the three parameters simultaneously, we first assumed that in each pair of observations, at least one density assessment is correct; as a consequence, if both observers provide the same estimate of the state of the site, that must be the true state of the site. Alternatively, this is equivalent to assuming that the values of P_{01} and P_{10} are low enough that simultaneous mis-estimation by both observers is rare. To put this in context, if the misclassification rates were 10% for both observers, simultaneous misclassification would affect only 1% of quadrats.

We secondly assumed that the probability of classifying state i as state j is the same as classifying state j as state i (i.e. $P_{ij} = P_{ji}$). This assumption is justified on the grounds that (i) the underlying density variable is a continuous one, hence the decision whether to assign state i or state j is likely to be arbitrary at the state boundary; (ii) frequently, the classification error will result from small variations in the GPS grid, which again will lead to arbitrary state misclassification.

These assumptions allow simultaneous estimation of all three parameters, as they rule out the possibility of high rates of correspondence between observers resulting from simultaneous misclassification. Under these assumptions, eqn 3 becomes:

$$P(0,0) = P_{00}^2 f_0 \qquad \text{eqn 5a}$$

$$P(1,1) = P_{11}^2 f_1 \qquad \text{eqn 5b}$$

$$P(0,1) = P_{00}P_{01}f_0 + P_{10}p_{11}f_1 \qquad \text{eqn 5c}$$

where $P_{00} = P_{11}$ and $P_{01} = P_{10}$. The log-likelihood for the data is then:

$$L = n_{00}\ln(P_{00}^2 f_0) + n_{11}\ln(P_{11}^2 f_1) + n_{01}\ln(P_{00}P_{01}f_0 + P_{11}P_{10}f_1) \qquad \text{eqn 6}$$

This quantity was maximized numerically using the 'optim' routine in R (R Development Core Team 2009), restricting the range of values searched to between 0 and 1 for all three parameters.

As noted above, the observed frequencies of 0 s and 1 s are biased relative to f_0 and f_1 as the observed frequency with which an observer assigns density state zero is:

$$P(0) = P_{00}f_0 + P_{10}f_1 \qquad \text{eqn 7}$$

Equation (7) makes clear that the estimated frequency of state 0 is dependent not only on the correct assignment of state 0, but also on the incorrect assignment of state 1. This is important because if the frequencies of the two states are very different, the observed frequencies may be highly biased.

Analysis of replicated surveys – multi-state data

The analysis of misclassification rates in multi-state data is complex (Royle & Link 2006). In the dataset we have, there are two observers independently censusing the same field assigning from five density states (zero, low, medium, high, very high).

To make the analysis tractable, we make the following simplifying assumptions. First, it is assumed (as above) that at least one observer classifies the state of each quadrat correctly (equivalent to assuming that error rates are sufficiently low that double misclassification is negligible). Second, we assume that errors of classification by each observer are not more than one density state greater or less than the true state. This assumption is justified because the observed difference between observers was greater than one density state in only 27 out of 2661 quadrats (i.e. only 1% of cases). Third, we assume that the probability of misclassification of one state as another did not exceed 0·5: although in the analyses reported below the estimated proportions did not approach this level, we enforced this condition for computational simplicity to ensure that net error rates for each state did not exceed 1. Finally, we assumed that the probability of classifying state i as state j is the same as classifying state j as state i; this assumption was required as the relatively small overall number of misclassifications (in total the observers classified 254 of the 2661 quadrats differently, ~9%) made it impossible to distinguish these, as this typically requires large number of misclassifications (see Collett 2003).

Following the same computational logic as described above, the log-likelihood for the data is, where n_{ij} is the number of quadrats in which the estimates of the two observers are different with one assigning state i and the other assigning state j:

$$L = \sum_{i=1}^{5} n_{ii}\ln(P_{ii}^2) + \sum_{i=1} n_{i,i+1}\ln(P_{i,i+1}P_{ii}f_i + P_{i+1,i}P_{i+1,i+1}f_{i+1}) \qquad \text{eqn 8}$$

The complication in estimating the parameters of this model is that there are a number of implicit constraints in operation. Specifically, for each density state, the probability of correct assignment (P_{ii}) and the probabilities of misclassification to states j and k (P_{ij} and P_{ik}) must sum to 1 ($P_{ii} + P_{ij} + P_{ik} = 1$); furthermore, the frequencies of the four density states must all sum to one ($f_1 + f_2 + f_3 + f_4 = 1$). To facilitate the estimation of the model parameters under these constraints, we re-parameterized the model. To do this, and given the assumption outlined above that the probability of misclassification of one state by another could not exceed 0·5, we replaced P_{ii}, P_{ij}, and P_{ik} by:

$$P_{ii} = 1 - P_{ij} - P_{ik}, \quad P_{ij} = \frac{0\cdot5\exp(\theta_{ij})}{1+\exp(\theta_{ij})}, \quad P_{ik} = \frac{0\cdot5\exp(\theta_{ik})}{1+\exp(\theta_{ik})} \qquad \text{eqn 9}$$

and f_1, f_2, f_3, f_4 and f_5 by:

$$f_1 = \frac{\exp(\phi_1)}{1+\exp(\phi_1)}, \; f_2 = (1-f_1)\frac{\exp(\phi_2)}{1+\exp(\phi_2)},$$

$$f_3 = (1-f_1-f_2)\frac{\exp(\phi_3)}{1+\exp(\phi_3)}, \; f_4 = (1-f_1-f_2-f_3)\frac{\exp(\phi_4)}{1+\exp(\phi_4)},$$

$$f_5 = 1 - f_1 - f_2 - f_3 - f_4 \hspace{3cm} \text{eqn 10}$$

The variables on the transformed scales are unbounded and not subject to any constraints, and there are eight free parameters to be estimated (f_1, f_2, f_3, f_4, P_{12}, P_{23}, P_{34}, and P_{45}). We found that the likelihood could not be reliably maximized using numerical methods and therefore estimated the parameters using a Bayesian Markov Chain Monte Carlo approach, assuming improper priors for the parameters and using a Metropolis sampling algorithm (using the MCMCmetrop1R function of the R package MCMCpack; see Bolker (2008) for an application of this function under the assumption of non-informative priors). This approach allowed us to obtain parameter estimates as well as distributions for these estimates. We estimated the parameters separately for each field and time period, comparing observations for the same observer repeatedly estimating the density state of each quadrat at different times, as well as different observers estimating density states at the same time.

EFFECT OF MEASUREMENT ERROR ON TRANSITION PROBABILITIES

It was impossible, within the time and resources available, to conduct replicated surveys routinely in each year. However, if levels of measurement error are relatively low and consistent between time periods, observers and different locations, estimates of census error from the trials designed to target different species and crops should prove adequate to control for measurement error in subsequent analyses. We used the data on *A. myosuroides* resurveyed in the same field in 2007 and again in 2008 to estimate state transition probabilities and to assess the effects of estimation error on these.

In exploratory analyses, we contrasted several approaches, including maximum likelihood estimation and MCMC methods. We found that of the methods we explored, the simulation-extrapolation method (SIMEX; Stefanski & Cook 1995) yielded consistent and unbiased parameter estimates with relatively little computational effort. This approach has the following rationale: extra measurement error is added to the observed data and the parameters of interest are 'naïvely' estimated in the data with added error. The systematic change in the naïve estimates of the parameters with changing levels of error can be examined and extrapolated back to estimate the parameters in the absence of error (Fig. 1 gives an example of this).

The specific method we used is termed misclassification SIMEX (MC-SIMEX) and is formulated following Küchenhoff, Mwalili, & Lesaffre (2006). If the misclassification matrix is termed $\mathbf{E}$ we define Λ^λ which is a transformation of $\mathbf{E}$ by a scalar parameter λ:

$$\mathbf{E}^\lambda = \mathbf{C}\Lambda^\lambda\mathbf{C}^{-1} \hspace{3cm} \text{eqn 11}$$

$\mathbf{C}$ is a matrix of eigenvectors of $\mathbf{E}$, and Λ is a diagonal matrix of eigenvalues. λ is assumed to be greater than or equal to zero and in the case that $\lambda = 0$, $\mathbf{E}^\lambda$ is an identity matrix, equivalent to a misclassification matrix in which there is no error. If $\mathbf{N}$ is the true set of density states and $\mathbf{N}^*$ is a misclassification of $\mathbf{N}$ according to $\mathbf{E}$, and if $\mathbf{N}^{**}$ is a misclassification of $\mathbf{N}^*$ by $\mathbf{E}^\lambda$, then it follows that $\mathbf{N}^{**}$ is related to $\mathbf{N}$ by the misclassification matrix $\mathbf{E}^{\lambda+1}$. The simulation step works by simulating added measurement error to the observed data $\mathbf{N}^*$, and recording estimated 'naïve' parameter values as λ is increased. The relationship between the naïve parameter estimates and λ is then extrapolated back to a value of $\lambda = -1$ to estimate the values of the
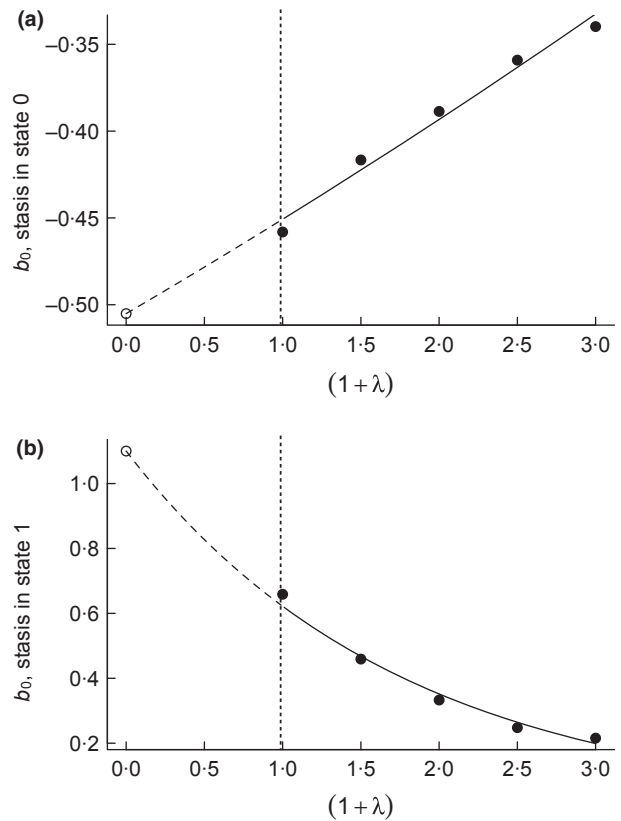

Fig. 1. An example of how misclassification SIMEX works. Data assuming relative error of 1 are extrapolated by adding error in order to generate a curve (solid line), and then simulated back to relative error of 0 (dashed line) to calculate the correct parameter estimates. (a) parameter measuring stasis in state 0; (b) parameter measuring transition from state 0 to state 1. Note that the parameters are taken from the GLM modelling the transition probability as a function of previous state, and hence are measured on the logit scale of the linear predictor.

parameters in the absence of error. We used linear extrapolation of the relationship between estimated transition probabilities and λ for values of λ close to zero to generate the MC-SIMEX estimates.

We estimated transition probabilities and the effects of error on these using a linear modelling approach. A GLM was used to relate the density state (0 or 1, coded as a binary variable) at time $t + 1$ to that at time t. A binomial error and logit link was assumed. The coefficients of the model were recorded, then the error in the data amplified in the manner described above. Figure 1 shows how this is applied to the model coefficients to generate corrected parameter estimates. Note that this is a better approach than using the 'naïve' observation of the proportion making the transition between states, as the GLM is fitted assuming a logit link and this ensures that fitted transitions lie between 0 and 1.

To generate a distribution of parameter estimates, the dataset was resampled with replacement 1000 times, and the MC-SIMEX applied to each resampled dataset. The distribution of parameter estimates was recorded to yield a sampling distribution about the mean.

Results

Figure 2 shows some examples of the survey data from different observers and at different times. It is apparent that the
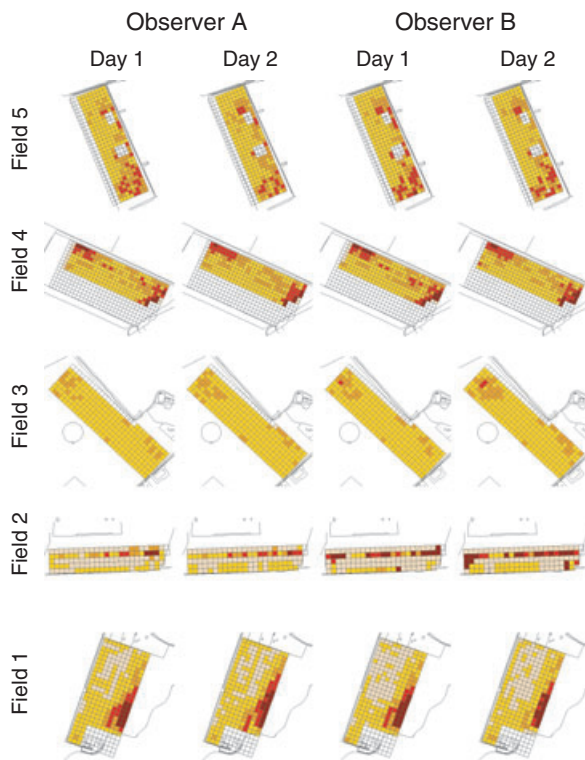
Fig. 2. Example data showing the distribution of weeds in five fields in Lincolnshire for two observers on two different days. Fields 1–3 show *Chenopodium album* in sugar beet, field 4 shows *Alopecurus myosuroides* in winter wheat, and field 5 shows *A. myosuroides* in field beans. Increasing darkness of colour indicates increasing density of weed per 20×20 m quadrat, from 0 to very high density. White quadrats were not surveyed.

density-structured method captures the variability in weed densities both within and between fields, and is also consistent between observers and days.

COMPARISON OF APPROACHES

Counts of weed numbers within cells assigned to density states showed high consistency (Fig. 3). For both *A. myosuroides* and *C. album,* there is a clear and statistically highly significant relationship between the assigned density state and the measured density of plants. The density states perform well at discriminating differences between the densities, with the 50% percentiles reasonably well separated, especially in *Alopecurus.* Note that in each 20×20 m quadrat, the area sampled for this analysis is only a fraction (6 m^2) of the total area (400 m^2), so a large proportion of the plot-to-plot variation about the mean for each state is likely to be sampling error (i.e. error in the estimate of the plot mean resulting from within-plot variability).

Most of the variation in density of *A. myosuroides* was the consequence of variations in attributed density state between quadrats (63% of deviance explained). A small proportion was explained by variations from field to field (7·3%) and, although statistically significant, only 9·9% of the variance in density

from quadrat to quadrat was attributable to the density state × field interaction (Table 2a).

In the case of *C. album*, analysis of the deviance indicated that a large proportion of the variation in density from quadrat to quadrat (39·5%) was attributable to between field differences in mean density. A similar proportion (34%) was attributed to plot-to-plot variance in density resulting from variations in density state, but little (4·8%) was estimated to be attributable to the density state × field interaction, and statistically non-significant (Table 2b).

QUANTIFICATION OF ERROR

The parameter estimates and (mis)classification rates returned by the Bayesian MCMC approach were generally narrowly distributed around the mean (for an example of the distribution of estimates, see Fig. 4).

The weed presence/absence surveys in winter wheat, wild oats and barley indicated that there was considerable correspondence between the density states estimated by independent observers (Fig. 5). Confidence limits for all comparisons were narrow, and the probability of correct classification and estimates of frequency were high and consistent between census times. For example, the correct assignment probability was estimated to be 0·93 for *A. myosuroides* in winter wheat, such that the error rate is only $\sim$7%. The estimated frequency of state 1 (f_0) was 0·05, which is considerably lower than the estimate of 0·11 from the raw data. This potential for such differences was pointed out above (eqn 7).

We similarly found that the estimated rates of correct classification were high in the data on fields surveyed in which multiple density states were present (Fig. 6). These were mostly $>$0·80 (except where small sample sizes prohibited accurate estimation of the values, for example for *A. myosuroides* in beans). This high rate of correct classification was consistent within and between observers and census days: confidence intervals for each of the four comparisons (observer 1 vs. observer 2 on both days 1 and 2; observer 1 on day 1 vs. 2, and observer 2 on day 1 vs. 2) were overlapping in almost all comparisons. The probability of misclassification was low, and appeared to increase slightly at higher densities. However, the frequency of higher densities was lower. Consequently, we conclude that the density state estimates are repeatable and robust.

ESTIMATING TRANSITION PROBABILITIES

The estimates of census error are important in generating robust estimates of transition probabilities in density structured models. In the analysis of the data on *A. myosuroides,* the MC-SIMEX indicates that there is bias in the estimates of the transition probabilities resulting from measurement error (Fig. 7). Without accounting for measurement error, the estimates of the transition probabilities are $t_{00} = 0.613$ and $t_{11} = 0.547$. In comparison, based on a linear extrapolation the MC-SIMEX estimates are $t_{00} = 0.631$ and $t_{11} = 0.622$.
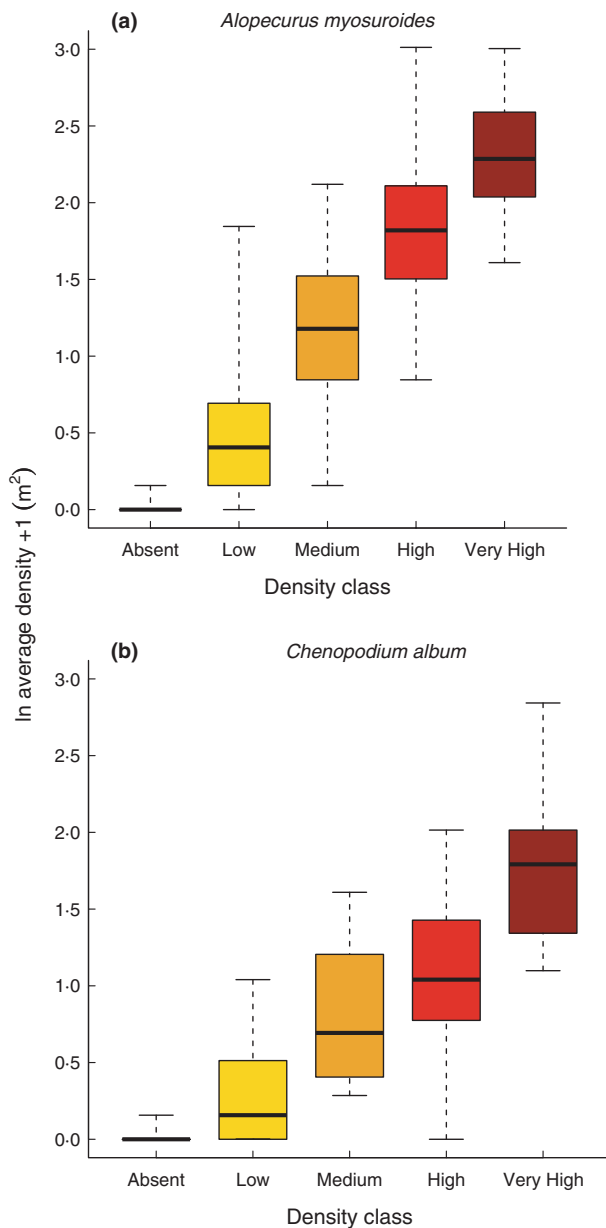
Fig. 3. Actual densities of two weed species in 1 m² quadrats of estimated density states in arable crops, visualized using box and whisker plots (minimum, lower quartile, median, upper quartile and maximum data values shown). Six 1 m² plots were randomly positioned in each of 255 20 × 20 m quadrats in 11 fields (*Alopecurus myosuroides*) and 75 quadrats in six fields (*Chenopodium album*). Box colours correspond to density states in Fig. 2.

There would therefore appear to be an appreciable bias in the estimate of P_{11}. In this example, the reason for this is very likely to be the low frequency of state 1 in 2007. The number of quadrats observed to be in state 1 in 2007 was only 8·8% (observer 1) or 11·3% (observer 2), with the MC-SIMEX of f_1 being 0·03. Consequently, the estimate of t_{11} has an extremely wide bootstrap variance (Fig. 7b) when compared with the estimates of the other parameters, which are very well estimated (Fig. 7).

Table 2. Variation in the density of (a) *Alopecurus myosuroides*, and (b) *Chenopodium album*, attributable to among-quadrat, among-field, and density state-field interaction terms. Results from generalized linear models with quasipoisson error and a log-link function

	d.f.	Deviance	Residual d.f.	Residual deviance	P
(a)					
Null			254	6136·8	
Field	10	448·2	244	5688·6	***
Density state	1	3854·9	243	1833·7	***
Field × density state	37	614	206	1219·7	***
(b)					
Null			74	1358·32	
Field	5	536·37	69	821·95	***
Density state	1	461·67	68	360·28	***
Field × density state	12	65·82	56	294·46	

Significance of model terms indicated by asterisks: ***$P < 0.001$

Discussion

Models are commonly used to investigate the processes that govern plant population dynamics. They are necessary to predict how populations will respond to perturbations such as climate change, introductions to new habitats, and to management (Bolker 2008). In this article, we have described and tested a new method for measuring and modelling plant populations. Estimates of population density obtained using this approach are robust and repeatable, and we have demonstrated that it is straightforward to quantify census error. Finally, we are able to use the approach to capture large-scale variation in population density successfully and discuss below how the approach can be developed.

Most studies of plant population dynamics use small-scale mechanistic demographic models that are costly to parameterize and prove difficult when attempting to account for measurement and observer error (Freckleton *et al.* 2008). We have described here a phenomenological model that is based entirely on estimates of plant density and makes no assumptions about the underlying processes. Our survey can pick up within-field variation in weed plant density (Fig. 2), and estimates of plant density are robust and accurately reflect the true density of plants in small quadrats (Fig. 3). Independent observers, although differing in their estimates, can provide comparable data on plant density with an error rate <10% (Figs. 5 and 6). Furthermore, using the density-state approach, it is easy to model observer error and correct estimates of the true density frequency using MC-SIMEX (Figs. 1, 5 and 6).

ADVANTAGES OF THE NEW METHOD

The density-structured approach offers several benefits in terms of data collection and analysis: (i) data collection is simpler than traditional techniques and is therefore more
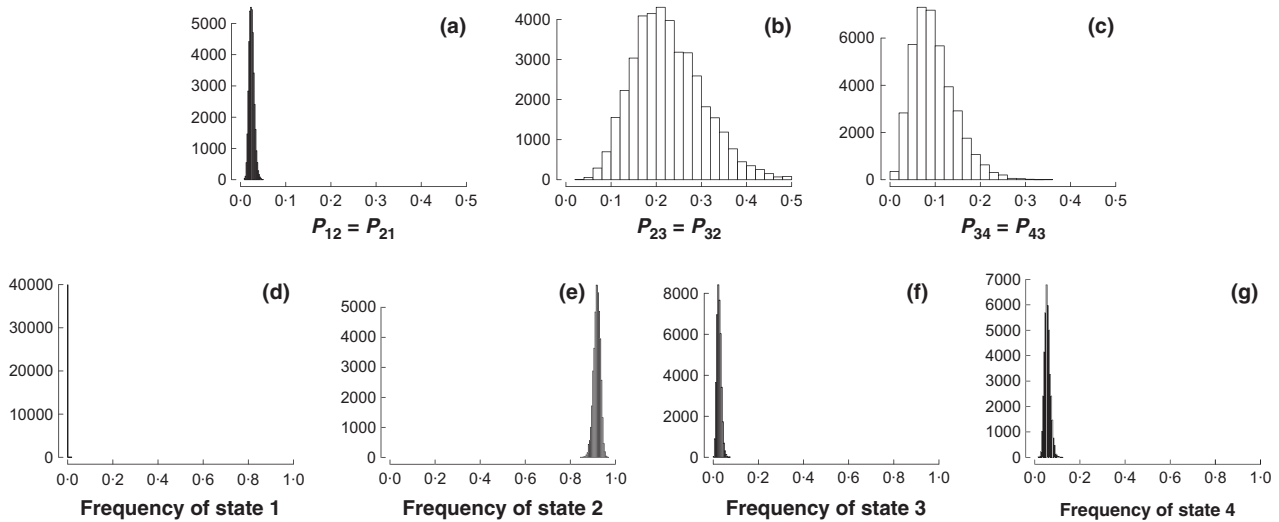
Fig. 4. Parameter estimates and (mis)classification rates: examples of distributions of parameter estimates and (mis)classification rates for *Alopecurus myosuroides* in a wheat field returned by the Bayesian MCMC approach. Frequency distributions of probabilities of classifying state 1 as state 2 and *vice versa* (a), state 2 as state 3 (b), and state 3 as state 4 (c). Probability distributions of frequency estimates for density state 1 to state 4 (d: no weeds; e: low weeds; f: medium weeds; g: high weeds).
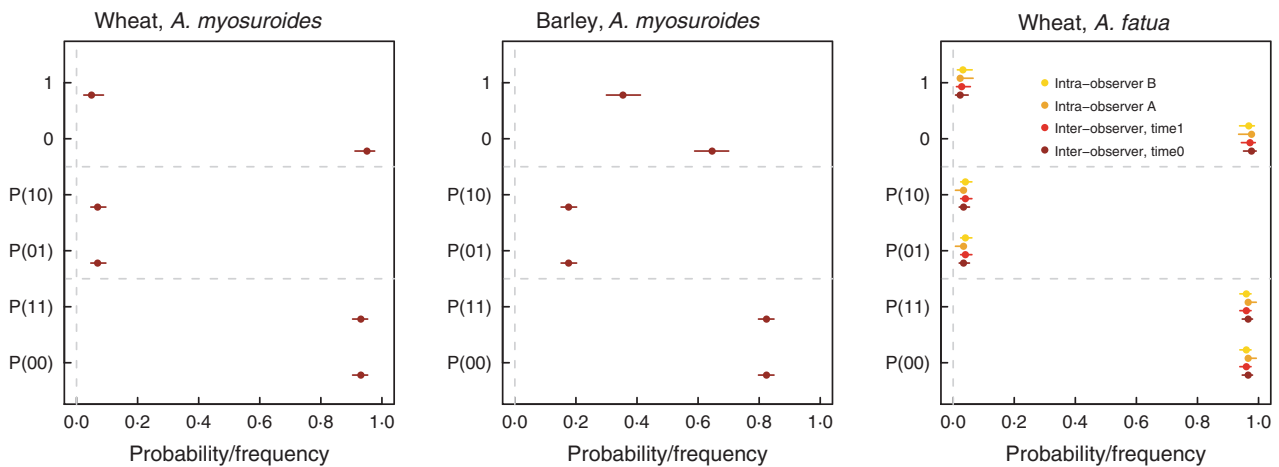
Fig. 5. Parameter estimates and probability or binomial state density models for two crops and two weed species (absent, 0; low, 1). Panes in each plot are divided by dashed lines: *Top* pane in each graphic shows estimates of frequency of each state. *Middle* pane shows the estimated probability of misclassification between observers or survey time. *Bottom* pane shows estimated probability of correct classification. Two observers repeated most surveys on 2 days, coded by colour (e.g. yellow = intra-observer error for observer 2; see legend). Fig. S3 is a grayscale version of this figure.

rapid; (ii) modelling techniques are robust and predictive; (iii) we can account for within- and between-observer errors; (iv) the models are phenomenological and make no assumptions about biological processes; (v) because of the speed of data collection, the techniques can be applied to problems at very large spatial scales that remained previously intractable.

The data collected using our techniques are substantially different from standard counts of plant densities. Density-structured models are much simpler, each sample unit being assigned a state from an ordered list of density categories. In our example, each quadrat was assigned a density state from one of absent, low, medium, high, and very high. In our dataset, the range of weed densities corresponding to these density

states were derived from previous count data, and as such, accurately reflected realistic ranges of densities. As individual plant count data are not required, data collection can be very rapid and large amounts of data over large spatial scales can be collected in a very short time. In the example discussed here, two field workers sampled about 4 ha in each of over 500 fields in 49 farms over 5–6 weeks. This amount of data and spatial extent is far in excess of most individual-based population studies.

We have shown above and elsewhere that the models are robust, accurate and reflect biological processes (Freckleton *et al.* 2011) and we can easily account for observer error (see below). Density-structured models are relatively simple compared with other individual-based models. As the
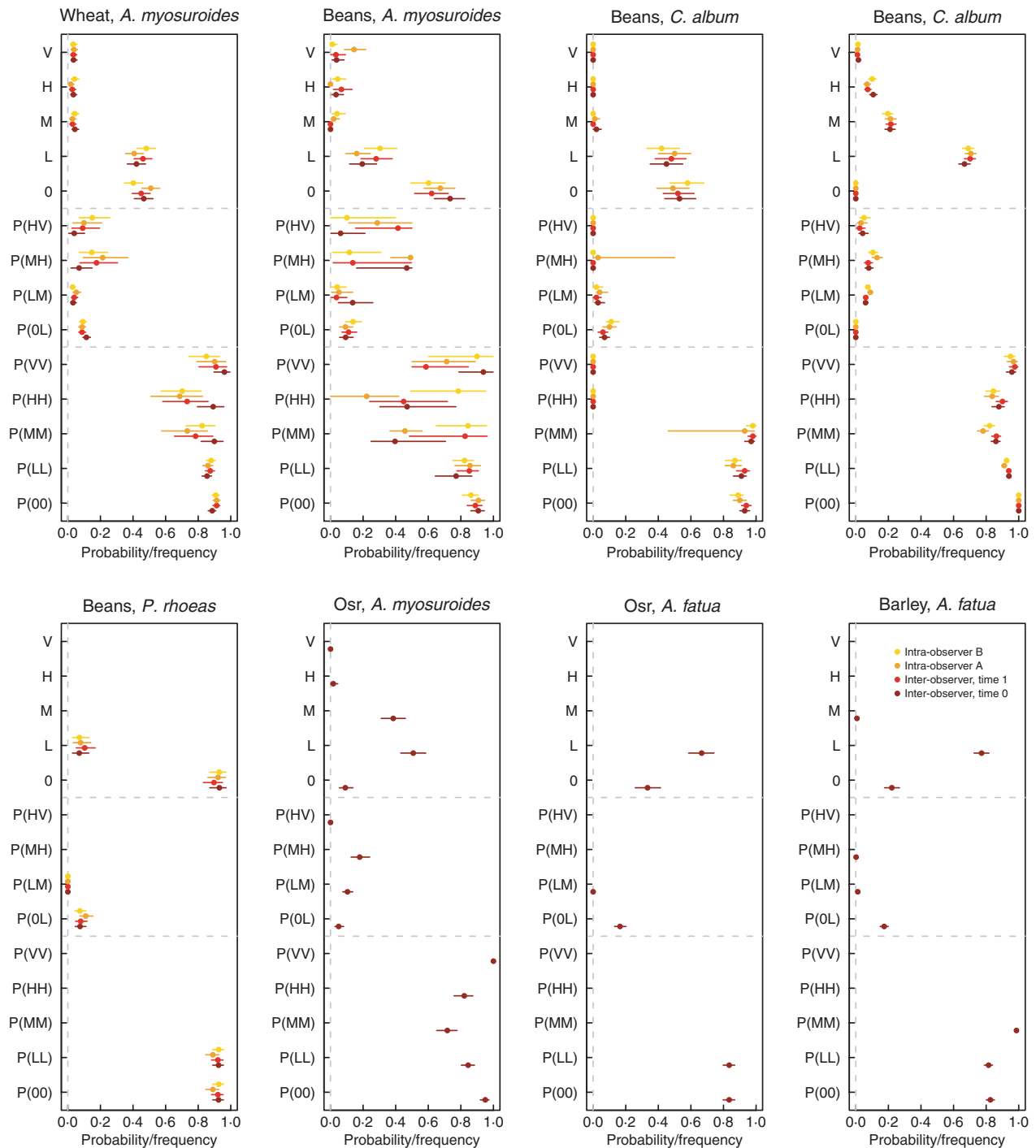
Fig. 6. Parameter estimates and probability (± 95% CI) of multi-state density state models for five density states (absent, 0; low, L; medium, M; high, H; very high, V), two observers and two observation times. Panes in each plot are divided by dashed lines: *Top* pane shows estimates of frequency of each state. *Middle* pane shows the estimated probability of misclassification between observers or survey time. *Bottom* pane shows estimated probability of correct classification. Two observers repeated most surveys on 2 days, coded by colour (e.g. yellow = intra-observer error for observer 2; see legend). Fig. S4 is a grayscale version of this figure.

density-structured modelling approach is phenomenological (modelling changes in observed weed densities), rather than mechanistic (relying on estimates of germination, survival, seed production to predict weed density), it is very easy to include other factors as explanatory variables of weed den-

sity, or include weed density as an explanatory variable itself, in other models. For example, one could generate aggregate results at various spatial scales: in our example, at the quadrat, field, farm, county and country scales. Furthermore, this hierarchical structure of the data leads very easily to analyses
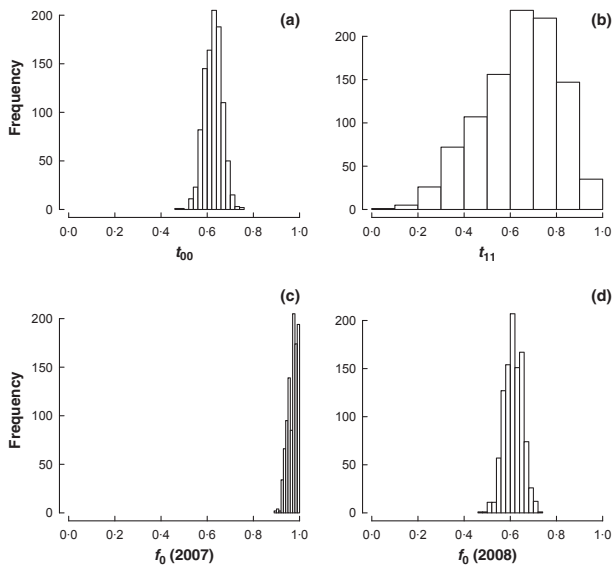
Fig. 7. Distributions of transition probabilities and frequencies of states from the MCSIMEX model, correcting for observer error. (a) Frequency distribution of bootstrapped transition probabilities for quadrats remaining in density state 0 in 2007–2008. (b) Frequency distribution of bootstrapped transition probabilities for quadrats remaining in density state 1 in 2007–2008. (c) Frequency distribution of estimates of density-state 0 in 2007. (d) Frequency distribution of estimates of density-state 0 in 2008.

of where most variation occurs. In our data set, for instance, we are actively examining how within-field variation compares with among-field, -farm, and -county variation in weed dynamics.

ACCOUNTING FOR OBSERVER ERROR AND BIAS

Few studies characterize variance in measurements resulting from observer error, although the issue has been understood for many years (Smith 1944). Of those studies that have compared the data collected by two or more independent observers, significant amounts of the variation in the data have been found to be caused by variation among observers (Leps & Hadincova 1992; Bergstedt, Westerberg, & Milberg 2009). This is especially true in studies that estimate vegetation cover (Sykes, Horrill, & Mountford 1983; Kennedy & Addison 1987; Vittoz & Guisan 2007; Milberg *et al.* 2008). Studies that record presence/absence of species tend to be less prone to observer error (Kirby *et al.* 1986; Ringvall *et al.* 2005).

Removing observer error in the collection process is virtually impossible. Given this, it is important to quantify it and account for error in subsequent data analysis. Quantification of observer error is a vital aspect of any biological monitoring study involving multiple researchers, and accounting for it will increase the utility of such long-term monitoring data (Legg & Nagy 2006). We showed that observer error has a significant but small effect on parameter estimates, and that multiple observers should be used to parameterize population models correctly.

INTEGRATION INTO MULTI-DISCIPLINARY RESEARCH PROGRAMMES

As density-structured models are not complex, including covariates or linking to other models is simple. This is important given the current emphasis on interdisciplinary studies and the inclusion of the anthropogenic interactions with the biological world. Efforts to link ecology, economics and sociology are often frustrated by a lack of common units of measurement or overly complex models in all these three spheres (Cooke *et al.* 2009). In this article, we have provided a simple and robust ecological model that can be readily linked to economic and sociological models with no loss of ecological information. With regards to this, we are currently linking our model with an economic model of farms, examining the feedbacks between weeds and farm management, and testing whether farmer preferences and behaviour determine weed dynamics in arable fields.

LIMITATIONS OF THE NEW METHOD

We acknowledge that our new method could initially appear unlikely to capture the dynamics of populations and may seem somewhat coarse. However, we have demonstrated here and elsewhere (Freckleton *et al.* 2011) that density-state models are accurate, robust and do capture population dynamics exceedingly well, with little loss of information. Given this evidence, we now address several apparent limitations to the new method we presented above, specifically that: (i) we do not make accurate counts of the number of individuals in populations; (ii) sample locations must be the same for every sampling time; (iii) it is difficult to apply the method to non-sessile organisms; (iv) the scale of the sampling quadrats and density states ideally must reflect the scale of biological processes under study; and (v) there are inherent issues of spatial autocorrelation between samples. These are not necessarily disadvantages of our approach, and demographic or other population models may be subject to similar issues.

In response to these perceived criticisms, first, we have demonstrated that accurate and robust models of population dynamics can be made using density-structured models that reflect the biology of the study organisms (Freckleton *et al.* 2011). Furthermore, estimates of population density can be returned from density-state models (Freckleton *et al.* 2011). Estimating density states allows for the rapid collection of large amounts of field data, which outweighs the small loss of resolution.

Second, permanent sample locations need to be identified to construct density-state models. As 'patch' or quadrat is the sample unit, rather than the individual, quadrats need to be easily relocated at each sampling time. It is usually much easier to relocate quadrats than individuals, and although there will be some error in this, especially if using GPS, this error can also be quantified and accounted for (see above). Alternatively, patch locations could be identified using physical features (e.g. a forest gap, or a lake).

Third, the method is mostly applicable to sessile organisms such as plants. Motile species, such as birds or mammals, could be modelled in this way if the sample quadrat was sufficiently large and the animals within easily quantified. Thus, aerial photographs of bird flocks, tracks, scat or other signs of animal presence could be modelled using density-state models. We have shown that bird populations can also be easily modelled in this way (R. Freckleton & D. Noble, unpublished data).

Fourth, the scale of the sample quadrat should match the scale of the organism and process under study. This will probably necessitate careful preliminary thought and work, but no more so than should precede any scientific study. In our case, we were able to take advantage of previous large-scale surveys to design our survey.

Fifth, spatial autocorrelation between density states of adjacent patches is likely, and can be addressed if required. We are currently working on modelling the spatial autocorrelation in our study system, and methods for dealing with spatial autocorrelation in general are well-established (Koenig 1999; Lichstein *et al.* 2002). The modelling framework can take the form of generalized linear models (Yee & Mackenzie 2002; Yee 2010), so it is easy to include covariates. In our case, with contiguous quadrats and spatially located fields and farms, autocorrelation can be easily modelled using freely available software (e.g. Rangel, Diniz-Filho, & Bini 2010).

Finally, the method described in this paper deals only with low-statured plants that are visible from standing human observers. There are many biological problems that cannot be addressed at this scale, but for which density-structured models are appropriate and that will require other forms of data collection (see below).

FURTHER APPLICATIONS OF DENSITY-STRUCTURED MODELS

Density-structured models are applicable to a wide variety of ecological questions, and should revolutionize long-term monitoring programmes and the study of population dynamics.

Quadrat size can be varied to accommodate any system of study, from global grids of longitude and latitude, to hectares of forest or quadrats of several centimetres for studying lichen recruitment. Quadrats could also be very different entities from those described in this study, including the water-filled floral bracts of *Heliconia* plants, bat roosting sites, networks of lakes or pools, and even countries or similar geo-political divisions.

The field methods used to collect density estimates in these diverse systems could include satellite images, reflectance spectra, aerial photographs, animal tracks, and even vocalization frequency. Our density-structured approach is particularly suited to long-term monitoring programmes, especially of organisms of conservation interest, where time and resources may be scarce. For reasons of the problems associated with gathering accurate information to parameterize mechanistic models discussed above, whereby small errors in parameter estimates can lead to wide variation in predictions, density-structured models could be used to monitor population dynamics very robustly. This is of great importance when considering rare species, where the probability of unseen individuals may be high. Accounting for observer error in the monitoring of rare species may be of critical importance for determining population success and assignation of categories of risk and rarity (e.g. CITES).

Density-structured models can also radically alter the way we monitor species' populations in response to large-scale global factors, such as changes in climate. Resources for science are always in short supply and limit the scope of many studies. However, using density estimates, many quadrats can be surveyed in a short span of time. Therefore, a large-scale network of quadrats spanning the full range of climate variables and/or the full extent of species ranges can be easily monitored. Variation in density as a function of differences in climate can be modelled and used to predict and monitor species responses to climate change.

Finally, this article represents only one way in which density-structured models could be developed. We presented a linear density-structured model framework and parameterized it phenomenologically. The more general idea of density structuring is not limited to linear models, nor are density-structured models necessarily parameterized phenomenologically. Taylor & Hastings (2004) used mechanistic parameters (vegetative growth rate) and a simulation model to estimate transition rates. Applying density-structured models in this case, or extending them to animal rather than plant species, might not be as easy to parameterize phenomenologically.

Conclusions

We have described a wholly integrated field and analytical method that is robust, accurate and predictive. Data analysis is computationally and analytically non-intensive, and allows for the estimation and inclusion of observer error. Covariates can be modelled using an extension of the generalized linear modelling framework and density-state models make no assumptions about the underlying biological mechanisms. Our new density-structured approach is ideally suited to addressing many urgent questions in ecology and should revolutionize the design of conservation programmes and long-term monitoring programmes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Data structure and sampling for arable weed survey.

Fig. S2. Histograms of weed densities per m^2 in FSE trials.

Fig. S3. Black and white version of Fig. 5. Parameter estimates and probability or binomial state density models for two crops and two weed species (absent, 0; low, 1).

Fig. S4. Black and white version of Fig. 6. Parameter estimates and probability ($\pm$ 95% CI) of multi-state density state models for five density states (absent, 0; low, L; medium, M; high, H; very high, V).

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